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AGE AND GROWTH OF *LOLIGO PEALEI*, A POPULATION STUDY OF THE COMMON ATLANTIC COAST SQUID¹

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Loligo pealei (Lesueur, 1821) has been the subject of continuing scientific interest, especially at the institutions in Woods Hole, Massachusetts. The species has supported a small domestic bait fishery amounting to about 1000 metric tons per year over the period 1879-1967 (Lyles, 1968). The Russians have investigated the possibility of developing an offshore fishery (Vovk, 1969) and the Japanese began a large-scale harvest of the species in the New York Bight with 14-15 vessels during the winter of 1969-1970. Bureau of Commercial Fisheries market news release indicated that the Japanese fleet took approximately 13,000 metric tons of *L. pealei* during a three month season in the first year alone. This greatly increased exploitation and a developing concern for marine populations in general require a practical means for aging *L. pealei* to facilitate studies of its life history.

A. E. Verrill (1882) reported on the rate of growth and size of *L. pealei* to refute what he considered a commonly held opinion that all squid are annual animals. This was the first quantitative contribution of its kind in squid biology and it exerted considerable influence on subsequent teuthological studies. Verrill based his report on a logical assemblage of size data from preserved specimens collected at various localities along the New England coast during the warmer half of the year. Recognizing the difficulty of identifying age groups among these specimens, he tabulated generous size ranges which suggest a single, diffuse class each year and a longevity of three or four years. Difficulty in confirming Verrill's suggested growth rate for young *L. pealei* has been reported (Summers, 1968). In my experience, Verrill's growth scheme lacks sufficient precision to be useful in analyzing the size structure of this species and introduces problems which are inconsistent with present knowledge of squid biology.

In general, squid lack nautral age markings (annuli), do not survive well in captivity (Summers and McMahon, 1970 and unpublished) and are poor prospects for ordinary tagging studies. As a result, reports on the growth of squid usually are based on their population dynamics. Commercial sources have frequently been employed in these studies with a probable introduction of sample bias (Tinbergen and Verwey, 1945; Mangold-Wirz, 1963; Fields, 1965 and others). Various statistics have been used to describe size classes of squid; in a probable series of increasing statistical reliability, these include: record size (Choe, 1966; Clarke, 1966), size range (Verrill, 1882; von Boletzky *et al.*, 1971), modal size (Tinbergen and Verwey, 1945; Rao, 1963; Haefner, 1964; Fields, 1965), mean size (Fridriksson, 1943; Squires, 1957 and 1967; Jaeckel, 1958; Mangold-Wirz,

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1963) and fitted size distributions (Murakami and Shindo, 1949; Summers, 1968). Size ranges are of little value without a knowledge of sample size, bias and distribution. Modal sizes must be interpreted and are subject to chance "noise" in the data. Mean sizes are inappropriate for mixed age groups and perhaps for mixed year classes. Finally, to be meaningful, fitted size distributions must reflect the biological events regulating natural size structure.

It was the purpose of this study to use population dynamics techniques for a new description of age and growth in *L. pealei*. Attempts to provide contrasts with reports in the literature are intentional in view of Verrill's precedent with this species. As far as possible, systematic sampling was employed. Gear of estimable sampling bias was used and the data were analyzed by a sensitive (non-prejudiced) statistical technique in an attempt to identify valid age groupings.

MATERIALS

Quantitative sampling of *L. pealei* extended from August 1967 to July 1970 and a qualitative survey continued into November of 1970. Except for newly hatched (planktonic) squid and materials used for comparative purposes, all samples resulted from daytime collections employing large otter trawl nets. Off-shore winter collections made between Georges Bank and Cape Hatteras in March and April of 1967 and 1968 were reported previously (Summers, 1969). Fifty-two collections were made during the inshore season (May through November) near Woods Hole; most of them in Menemsha Bight in southern Vineyard Sound (a description of this station appears in Summers, 1968). Inshore collections were made in all three years with either a #35 otter trawl or a 45-65 Long Island Sound balloon trawl (Summers, 1968; Summers and McMahon, 1970). Planktonic squid were taken near the surface with one-half meter plankton nets (860 micrometer mesh size) on several occasions in July and August 1967-1969. Subsurface collections of planktonic squid were made with a six foot Isaacs-Kidd midwater trawl (fine mesh cod end) on July 17, 1969 and with paired, one-fifth meter "bongo" nets (505 micrometer mesh size) on July 2 and 14, 1970.

Squid collections from some large catches were subsampled volumetrically, *i.e.*, a large portion of the catch was spilled over a sample bucket which held a minimum of 50 adult squid. All measurements and dissections were made on fresh, unpreserved animals. Dorsal mantle length was recorded to the nearest whole centimeter, sex and sexual maturity were noted for every individual excepting young-of-the-year squid with dorsal mantle lengths less than about six centimeters. Males were considered mature if spermatophores were present in Needham's sac (spermatophoric sac) and females were classified mature if the ovary was expanded and loose eggs were found in the oviduct. These maturity indices are potentially more subjective for females than for males and are not considered a positive indication of breeding activity at the time of capture. During the breeding season, we recorded as mature a number of small squid (10 cm dorsal mantle length or less) which may not have participated in the breeding activity and probably could not have produced a full complement of fertilized eggs without further development. Records of 15,132 squid resulting from the above sources were utilized in this report.

Several miscellaneous collections were used for comparative purposes. These resulted from the operation of a fishtrap (Summers and McMahon, 1970), squid jigging under lights, stomach contents of predatory fish and trawl samples from surveys conducted by the Bureau of Commercial Fisheries (now, National Marine Fisheries Service).

METHODS

Data from each sample were tabulated in one of three categories: (1) males, (2) females and (3) young-of-the-year squid. Individuals in the last category were all sexually immature and generally were not sexed; occasional dissection, however, indicated a consistent 1:1 sex ratio. Further analysis was carried out when data from twenty or more squid were present in a particular category. The actual numbers of collections analyzed and average numbers of specimens per category, respectively, for the inshore sampling were as follows: males, 39 and 56.3; females, 34 and 58.6; young-of-the-year, 27 and 157.3. All categories were not sufficiently numerous to qualify for inclusion in each collection, so the inshore data represents 45 collecting dates and 8,437 squid distributed over three, 7 month periods.

Size data were subjected to a size class separation using the method described by Harding (1949) and extended by Cassie (1954). Polymodal frequency distributions were graphically fitted by normal distributions on probability paper, providing estimates of mean, standard deviation and relative abundance for each mode. Normal size distributions were assumed for sexed squid and lognormal distributions for young-of-the-year squid to accommodate a positive skew in their sizes (Summers, 1968). Mean and logmean mantle lengths were weighted by the relative abundance for analysis and standard deviations were compared for consistency of class separation. Weighted mean sizes were tabulated for each size class by category; these were pooled by cruise for the winter collections and by month for inshore sampling. Initial phases of a second size class separation were carried out on the pooled data to locate intersections between major size clusters at different times of the year. Winter data were not considered to be weighted comparably to inshore collections because of differences in fishing gear and depth stratification of *L. pealei* in the winter (Summers, 1969); their use was restricted to qualitative aspects in further analysis.

RESULTS

Results of the data treatment are summarized in Figure 1. Heavy vertical lines in the figure represent the monthly range of size class means and oblique lines bordering the stippled area indicate the intersections of principle size clusters (results of the first and second size class separations, respectively). Age groups are identified by size clusters under the assumption that breeding is seasonal. Age is inferred by following population growth backward in time to hatching. Quantitative data in Figure 1 are a composite for males and females assuming a 1:1 sex ratio (the approximate ratio of male and female categories in all collections). The per cent occurrences of different inferred age groups is shown in the figure for the sexed categories. Young-of-the-year squid below the size of seven

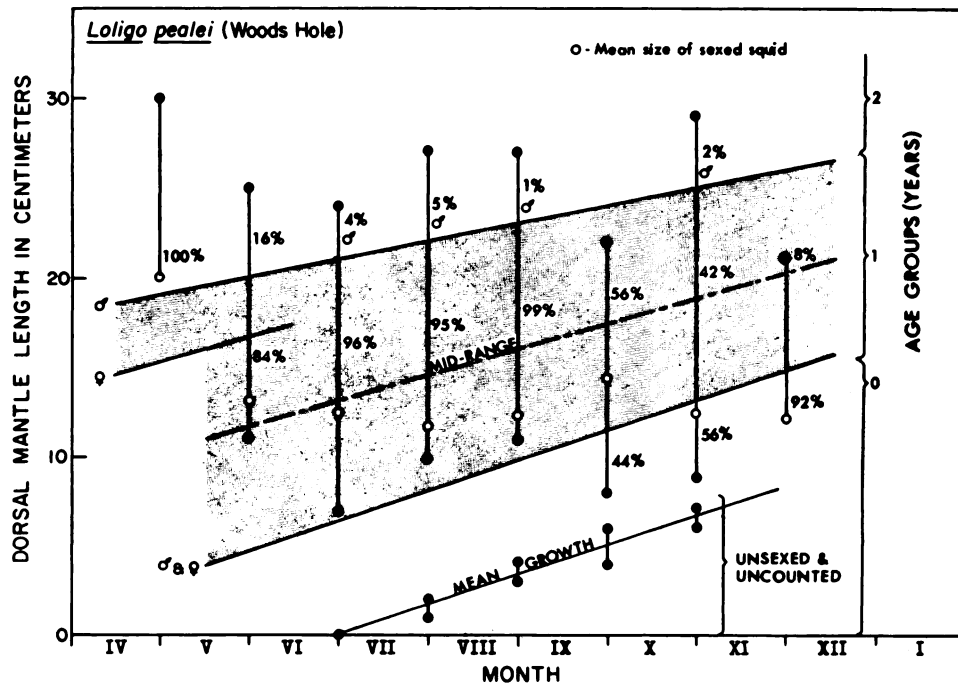


FIGURE 1. Monthly range of size class means, proposed age groups and occurrences of age groups near Woods Hole, Massachusetts. The data represent 8,437 squid from 45 collections in the years 1967-1970 and are a composite for males and females assuming a 1:1 sex ratio. The range of sizes for one year olds has been stippled for emphasis. Open dots indicate the mean size of all sexed squid (those with a dorsal mantle length of seven centimeters or larger). See text for further interpretation of the figure.

centimeters were specifically excluded from the quantitative results because they were generally a distinctive size class, their relative abundance was known to increase markedly over the inshore season (Summers, 1968) and because of probable escapement (reduced efficiency of the trawl net in collecting smaller squid).

Open dots in Figure 1 indicate the mean size of sexed squid; this value is remarkably constant after the middle of May and stays within the range 11½ to 14½ cm for seven months. The mean size can be misleading because it includes both sexes and varying proportions of different age groups. Sexual dimorphism in mantle length has been reported for *L. pealei* (Verrill, 1882; Haefner, 1964); our results indicate that males exceed the length of contemporary females by 0.5 cm at nine months, 2.0 cm at 12 months and 4-5 cm at 20 months. The mean size is useful in comparing unbiased samples of *L. pealei* with no segregation other than the exclusion of young-of-the-year individuals.

Three age groups are shown in Figure 1. One year olds (age group 1) are intermediate in size and age among these groups and most numerous among the sexed squid over the inshore season; the range of their size class means has been stippled in the figure for emphasis. Two year old squid arrived inshore near Woods Hole around the first of May. Two year old females were not taken

after mid-June and only a minor proportion of two year old males were encountered after that date. One year olds arrived in large numbers in the latter half of May and remained to merge in size with the largest young-of-the-year squid by October. All two year old squid and almost all one year olds (into the month of August) were sexually mature and apparently breeding. Sexual maturity of one year olds decreased dramatically around the first of September. The majority of the young-of-the-year squid hatched around the first of July, these remained sexually immature and showed steady growth until the last squid migrated offshore in the latter part of November. Miscellaneous inshore samples were comparable to inshore trawl samples and no significant sample bias is indicated for sexed squid. In the winter collections, all female squid and most male squid below the size of 17 cm (*i.e.*, those less than two years old) were sexually immature (Summers, 1969).

DISCUSSION

Verrill's growth scheme for *L. pealei* can easily be imposed on the data presented in Figure 1. The broad range of sizes encompassing one year old squid can be readily identified and the absence of three or possibly four year old animals can be dismissed on the basis of rarity or possible avoidance of trawl nets. Verrill (1882) reported males of this species reaching a size of 42.5 cm, Summers (1968) noted a male 46.5 cm long and Vovk (personal communication) indicated that he had measured a male 45 cm long from offshore collections. Thus, larger (older) male squid exist in the population and the present data would seem to fall within Verrill's expansive life history model for *L. pealei*.

The size range indicated for one year olds (height of the stippled area in Figure 1) is particularly troublesome in applying Verrill's growth scheme. This range (approximately 13 cm) is conservative because it is a range of size class means and does not account for dispersion around those means. Given a continued growth of 1.8 cm per month, the rate observed for young-of-the-year squid (Summers, 1968), this range of sizes would have to result from a hatching period extending over at least seven months. A reduction in the growth rate over the first year would suggest a longer extrapolated hatching period. As noted above, mature female squid were encountered principally over a four month period; these included two age groups initiating breeding as much as one month out of phase with one another which produce a discrete brood near Woods Hole. Hence, the one year olds must represent a mixing from broods including some not observed near Woods Hole.

Reference to winter collections is instructive at this point. In March and April, *L. pealei* is concentrated near the continental shelf break and probably is compressed latitudinally from its summer range (Summers, 1969). Qualitative evaluation of the size distribution of winter squid clearly shows two size classes which, by extrapolated growth, would fall within the one year old size range given in Figure 1. These have modal sizes of approximately 8 and 14 cm dorsal mantle lengths. The smaller class was encountered in shallower depths from the southern mid-Atlantic Bight, it appeared to be the biological equivalent of the last young-of-the-year squid taken near Woods Hole, four months earlier. These I assume are a southern brood which probably hatches annually about the first week of

November. The larger class is identified clearly as the July brood shown in Figure 1. Cassie's technique did not indicate an intersection between these two broods at one year of age and the mid-range is tentatively used in Figure 1 to suggest their respective size ranges.

Data from the two broods have been synthesized and smoothed to produce the inferred growth scheme listed in Table I. Seasonal cycling of growth was

TABLE I
Growth scheme of Loligo pealei

Age (months)	Date, first of month		Mean dorsal mantle length (cm)	
	July brood	November brood	Females	Males
0	July	Nov.	0.2	0.2
2	Sept.	Jan.	4	4
4	Nov.	Mar.	7	7
6	Jan.	May	10	10
8	Mar.	July	12	12
10	May	Sept.	14	15
12	July	Nov.	16	18
14	Sept.	Jan.	18	21
16	Nov.	Mar.	20	23
18	Jan.	May	21	25
20	Mar.	July	23	28
22	May	Sept.	25*	30
24	July	Nov.	27*	32
.
.
34-36?	May-July	—	—	45

* Extrapolated from the observed data.

not apparent in the data and none is indicated in the progression of listed mean sizes in the table. Sexual dimorphism can be calculated as the difference in mean sizes of contemporary male and female squid. The growth scheme suggests a decrease in monthly growth rate from 1.8 cm (young-of-the-year squid) to 1.1 cm for males and 0.9 cm for females over approximately a one and one-half year period. Based on winter samples (Summers, 1969), these data indicate weight doubling about every four months.

The two-brood scheme is especially useful in explaining biological observations such as the proximity of sizes of certain one year old and two year old squid, the relative constancy of mean sizes of sexed squid and the rapid change in sexual maturity of one year olds around September first. Furthermore, a number of species of squid are known to die soon after breeding, including the closely related *Loligo opalescens* from California (McGowan, 1954; Limbaugh and Shepard, 1957; Hobson, 1965; Fields, 1965). Data are lacking to demonstrate a breeding induced mortality in *L. pealei*, but should such a mortality exist, Verrill's growth scheme could not be reconciled with the observed breeding population.

Counterparts of this growth scheme are not uncommon among other species of *Loligo*. The European squid, *Loligo vulgaris*, is reported to have a single

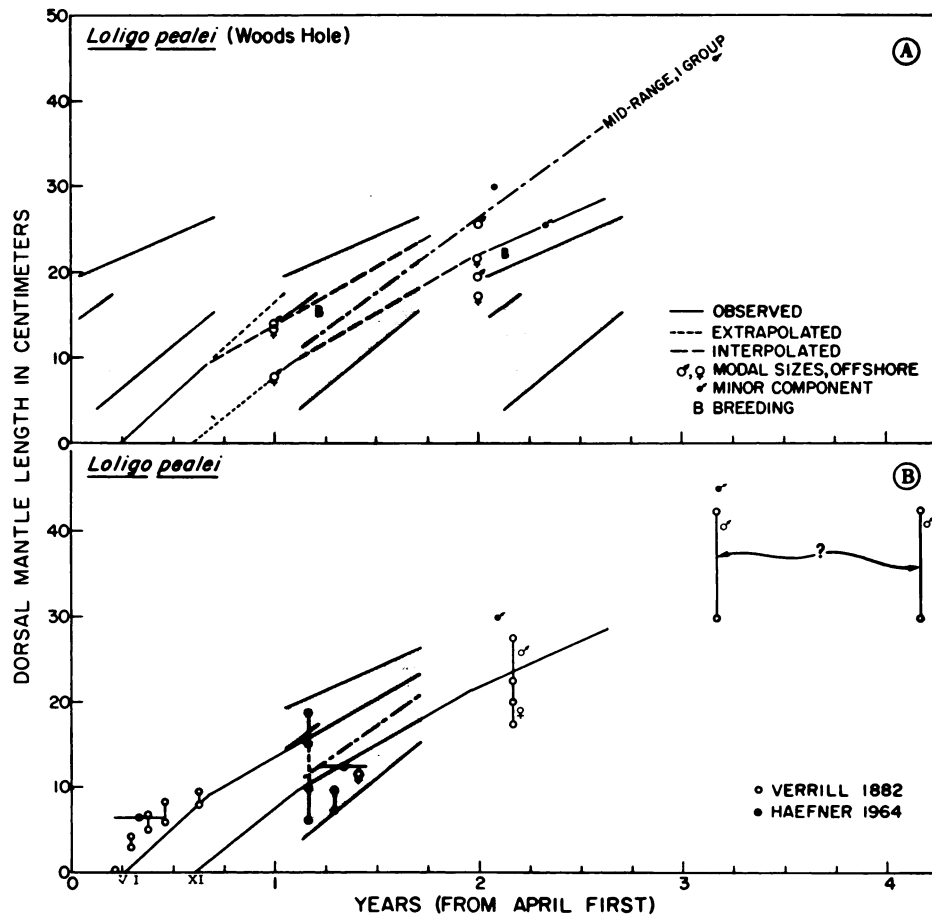
hatching period in the North Sea during the month of June (Tinbergen and Verwey, 1945) and both June-July and fall hatches (if not year-round hatching) in the western Mediterranean (Mangold-Wirz, 1963). Fields (1965) reported a year-round hatch of *L. opalescens* is probable off California with a peak period in the month of May. In the southern hemisphere, *Loligo brasiliensis* is reported to breed from November through March (de Castellanos, 1967; de Castellanos *et al.*, 1968). Thus, squid of this genus tend to have a peak of breeding activity in the spring and, where temperatures are moderate, have a second breeding period in the fall with a tendency toward year-round breeding.

It follows that the size structure of *L. pealei* sampled near Woods Hole is composed of six elements. These are: young-of-the-year squid (July brood), one and two year olds (both broods each) and a very few three year old males (July brood?). The older squid migrate inshore in decreasing order of size and age, two year olds by May first and one year olds by June first. The July brood is represented among two year olds by a minor portion of the early arriving males, the remaining males and all of the females appear to be the product of the younger November brood. The July brood of one year olds is replaced by November squid beginning in August with the greatest transition taking place around September first as indicated by the decreasing proportion of sexually mature animals. In November, many of the one year old males begin to exhibit a white coloration of the vas deferens which portends developing sexual maturity.

Older groups are probably replaced by serial inshore migrations and mortality after breeding. The occurrence of males 22 to 24 months old (and a very few as much as three years old) when females do not ordinarily live 20 months suggests that males may be less subject to breeding mortality. The net survival advantage of males cannot be too great, because imbalanced sex ratios were not observed in the sampling. This paradox could result from competition for females leading to postponed breeding among the males. Arnold (1962) reported that the largest male squid were the first to breed under laboratory conditions.

Mortality of *L. pealei* is difficult to estimate because all age groups cannot be adequately sampled at any one place or time. We have not detected strong year classes in our brief sampling and have regularly noted an inverse relationship between age and abundance. Sexually mature female squid bear between 3500 and 6000 eggs (depending on their size) which appear to approach 100% hatch in nature. For the population to remain stable, these eggs must replace two individuals if both sexes breed only once in a lifetime and there is no net recruitment. Under these assumptions, the annual survival of the June breeding population is approximately one in two thousand at its lower level.

A positive skew in the size distribution of young-of-the-year squid sampled near Woods Hole allows some refinement in the mortality estimate. The skew cannot be related to temperature lability in embryonic development (McMahon and Summers, unpublished). A lognormal model readily fits the observed distribution (Summers, 1968). (The same model seems appropriate for *L. brasiliensis* as reported by de Castellanos, 1967; de Castellanos *et al.*, 1968.) The tail of the observed size distribution must result from early breeding, probably by two year old squid. As shown in Figure 1, all of the *L. pealei* taken in the month centering on the first of May and one-sixth of those in the following



month were two year olds. Perhaps one-fourth of the egg deposition around June first was carried out by two year old females. Approximately 10% of the brood hatching ahead of the normal distribution would produce the skew size distribution. Thus, two year olds (mostly 18 and 19 months old) probably account for less than one-quarter of the total breeding population and contribute no more than one-third of the brood.

Interbreeding between age groups is likely. In the laboratory, older males frequently breed with younger females and the natural age structure suggests the same is true in the field. Interbreeding of this sort should have no net effect on the proportions stated above. Unfortunately, these data cannot be used to estimate the survival from 11 months of age to 19 months because different broods are involved and recruitment is apparent for at least one of them. It is consistent to suggest that *L. pealei* is mainly annual and that mortality follows breeding in both sexes. Sexual maturity is deferred in some members of the November brood and sexual regression need not occur.

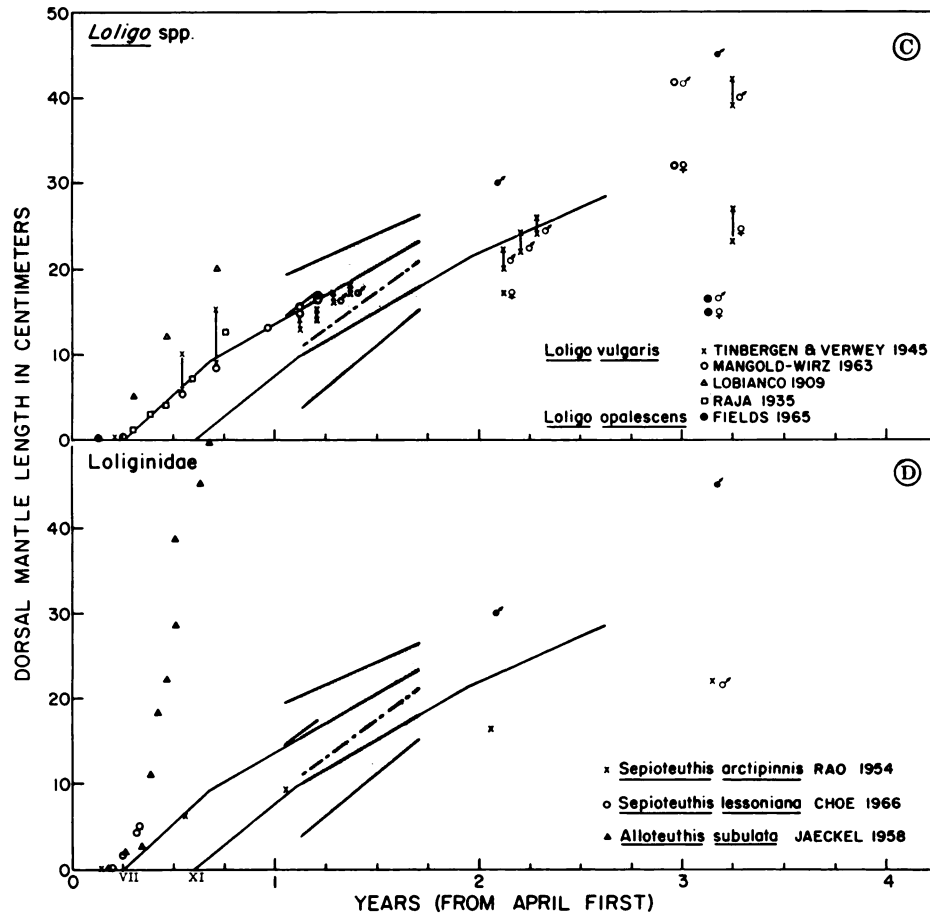


FIGURE 2. Shown in Figure 2A is a summary of the proposed growth scheme for *L. pealei* representing data from 15,132 squid. The range of sizes for one year olds (stippled areas) and mean growth of young-of-the-year squid are reiterated from Figure 1. A skeletal abstract of Figure 2A is repeated in Figures 2B-2D with data from the literature; these are arranged by taxa as indicated. Tinbergen and Verwey (1945) reported ventral mantle lengths which are slightly shorter than corresponding dorsal mantle lengths.

The growth scheme presented here can be used to anticipate latitudinal differences in age structure. One can postulate that two year olds (or older squid) would be rare or absent in areas where a significant November hatch occurs, especially south of Hudson Canyon. This tendency should be reflected by truncated ranges of size class means and lower mean sizes of sexed squid when compared to the data shown in Figure 1. The northern range limit of *L. pealei* has been recently described as coastal, southern Nova Scotia and the Bay of Fundy (Mercer, 1970). Squid taken as far north as the Bay of Fundy probably reflect selection for the capacity to make a long migration from the wintering grounds (Summers, 1969) and may show higher mean sizes. Stevenson (1934) observed the occur-

rence of *L. pealei* at St. Andrews, New Brunswick (Canada) "early in the summer" of 1932. He reported a peak abundance in a weir about mid-August and breeding activity in late August. Dr. and Mrs. Kay Petersen (personal communication) found egg masses and at least one newly hatched *L. pealei* in Minas Basin, Bay of Fundy late in the summer of 1970. These spotty data suggest that the "July brood" is delayed that far north.

A summary of the inferred growth scheme, winter data and major features of the inshore collections are shown in Figure 2A. Except as indicated in the figure, the information applies to a statistical intersex squid. A skeletal abstract of Figure 2A is repeated in Figures 2B, 2C and 2D for comparison with data from the literature on different genera and species of squid. Verrill's (1882) tabulated size ranges are shown in Figure 2B. Verrill listed a split range of sizes for one year olds which corresponds with the two broods suggested here. The simplicity of his one brood growth scheme is apparent in the figure. Haefner (1964) pooled the size distribution of squid collected over the period June 10 to September 17, 1958 in Delaware Bay; modal sizes from these data are shown in Figure 2B. Haefner's squid (like Verrill's) appear to have hatched earlier than those sampled recently near Woods Hole. His most distinctive older size class was a group of females which I would identify as the previous November brood (7 to 10 months old in his samples). Not shown in Figure 2B is yet another interpretation of the growth of *L. pealei* by Jaeckel (1958), who suggested an arbitrary reduction in the assigned age of Verrill's older groups. This modification is not supported by original data, but suggests that a higher growth rate might be appropriate.

As shown in Figure 2C, data describing the growth of *L. vulgaris* can also be fitted by the growth scheme presented here for *L. pealei*. Exceptions include Lo Bianco's (1909) data and the three year old females in Tinbergen and Verwey's (1945) report. Most recent authors have noted similarity in life history aspects between *L. pealei* and *L. vulgaris* and this certainly extends to their age and growth.

Fields (1965) indicated a uniform growth rate for *L. opalescens*, the end points of which are shown in Figure 2C. In view of the reports cited above, it is likely that Fields overestimated the age of *L. opalescens* and that he was dealing with an annual population.

Data for three other loliginid squid are shown in Figure 2D. It should be noted that *Alloteuthis subulata* exhibits an exceptionally long mantle length for its body proportions due to the development of a pointed projection on the mantle. None of the data shown in Figure 2D offer a useful contrast with the growth scheme of *L. pealei*.

Growth models for three species of *Loligo* can be grouped in four types: linear (*L. opalescens*, Fields, 1965); cyclic (*L. vulgaris*, Tinbergen and Verwey, 1945); von Bertalanffy (*L. pealei*, Verrill, 1882) and non-asymptotic (*L. vulgaris*, Mangold-Wirz, 1963; *L. pealei*, Summers, this report). The first of these is useful over short increments of time or in the absence of more complete information because it probably does not correctly describe the growth. Cyclic models are difficult to compare and lead to speculation about the effects of migration or selective mortality in the sampled population. The absence of reliable age mark-

ings in squid and apparent continued growth through cold seasons tend to rule out growth cycles. The last two models differ mainly in their degree of non-linearity and I have arbitrarily separated them on a basis of a factor of two in the growth rate. The von Bertalanffy (1934) growth model shows a wide change in instantaneous growth rates and indicates an approach to an asymptotic size during the animal's life span. Non-asymptotic models suggest that the oldest animals are still actively growing as is generally true for mollusks (Van Cleave, 1934; Russell Hunter, 1961). The applicability of these various models would be most convincingly demonstrated through studies of individual squid, especially by the results of tagging studies or prolonged laboratory maintenance.

The author wishes to acknowledge the assistance of many individuals who have contributed to this study in various ways from 1966 to the present time. Some of these have been cited in earlier papers as appropriate in specific phases of the work. I am indebted to my assistants, Miss Paula Mogilni, Mr. Steven Slomka, Mr. Michael Soukup and Mr. John McMahon, for their patience and hard work. I especially appreciate the stimulation, support and guidance provided by Drs. H. Burr Steinbach, Daniel L. Gilbert and John M. Arnold, all of the Marine Biological Laboratory. Finally, I wish to thank Mr. McMahon and Drs. Leland W. Pollock and Melbourne R. Carriker who read and criticized the manuscript.

SUMMARY

1. This paper describes the population size structure, inferred age, growth, reproduction and longevity of the common Atlantic Coast squid, *Loligo pealei*.

2. The sampling includes records of size (dorsal mantle length), sex and sexual maturity of 15,132 squid taken from 1967-1970. Nearly half of these were collected offshore between Cape Hatteras and Georges Bank in the late winters of 1967 and 1968. The remainder, including planktonic, young-of-the-year squid, were trawled in the vicinity of Woods Hole, Massachusetts between May and November of all three years.

3. Size classes were identified and weighted through the use of size frequency analysis and arrayed to provide an empirical growth model. Mean sizes of individuals appeared to increase smoothly to 16 and 18 cm at one year and 27 and 32 cm at two years for females and males, respectively.

4. Two broods arise each year, a ubiquitous July brood (probably delayed north of Cape Cod) and a November brood which probably originates in the southern mid-Atlantic Bight. Sexual maturity and breeding have not been observed at less than one year of age; at Woods Hole these features occur at different ages and slightly different dates for the two broods. Competition for females may postpone the breeding of some males and exaggerate the population sexual dimorphism.

5. The stock is basically annual, though a significant proportion of the squid hatching near Woods Hole appear to be the product of two year olds. A breeding induced mortality is consistent with the growth scheme for both sexes.

This mechanism is evoked to explain the dynamics of age structure and sexual maturity during the inshore season.

6. Maximum longevity is understood tentatively to be 36 months for males (more frequently 20–24 months) and 19 months for females. Sex ratios were consistently close to 1:1 though not necessarily balanced in older age groups.

7. The proposed growth scheme provides an hypothesis for latitudinal variations in the stock of *L. pealei*.

8. The results are compared with Verrill's influential treatment of the species and found to differ principally in the interpretation of data. The proposed growth scheme appears to be applicable to published data for the European squid, *L. vulgaris*, and is contrasted with records from other loliginid squid.

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